PART I INTRODUCTION TO FLORAL DIAGRAMS

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Introduction to flower morphology

1.1   Definition of flowers

Flowers were defined in many different ways in the past and there is no general agreement about how a flower should be defined. In the past there was emphasis on two main contrasting hypotheses (reviewed in Bateman, Hilton and Rudall, 2006). The pseudanthial hypothesis accepts that flowers evolved from a branched, multiaxial structure, i.e. a condensed compound inflorescence (e.g. Eichler, 1875; Eames, 1961). This means that a flower is an assemblage of separately functioning entities that became grouped together. The euanthium hypothesis stated that the flower evolved from a simple uniaxial (euanthial) structure, i.e. a condensed sporophyll-bearing axis with proximal microsporophylls and distal megasporophylls (e.g. Arber and Parkin, 1907). Floral organs all have attributes of leaves, and leaf-like elements, such as stipules, leaf bases, petioles and blades, occasionally appear in flowers (e.g. Guédès, 1979). More recently, phylogenetic studies have supported the theory that flowers evolved once and that all flowers are thus homologous ('anthophyte hypothesis' reviewed in Bateman, Hilton and Rudall, 2006). The theory is supported by evolutionary developmental evidence that the same genes are acting on the flower and vegetative shoot, and that the flower is best interpreted as a short shoot with specialized leaves (Glover, 2007).

More specifically, a flower can be defined a determinate structure with a generally defined number of organs; it bears both staminate and pistillate parts and organs are set in four series: sepals, petals, stamens and carpels. However, several angiosperm flowers lack these defining features, and differentiation of a perianth or limits of flowers and inflorescences are often unclear. The definition of flowers implicitly refers to angiosperms, but should also include

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gymnosperms. The gymnosperm cone could also be described as a flower, though the organization of the cone is generally unisexual. A defining character for angiosperms is enclosure of ovules by carpels (angiospermy), separating the flowering plants from their closest relatives (gymnosperms). Flowers are usually grouped into inflorescences that may be simple to highly complex, and are – at least in bud – often subtended by a specialized leaf, the bract, together with one or more (generally two) smaller leaves (bracteoles) placed in a lateral position. In monocots, there is another single adaxial bract instead of the two bracteoles. Bracts and bracteoles are absent in some species, and this can influence the position of organs in the flower. In some groups of plants the limits between bracts and floral parts are unclear. The inflated axis, called a receptacle, bears floral organs in spirals or in whorls (or a mixture of both). The outer floral organs are sterile leaves called a perianth. When undifferentiated they are described as tepals. More often, there is differentiation into an outer whorl (calyx or sepals) and an inner whorl (corolla or petals). The androecium, or the totality of stamens bearing microsporangia, can be organized in a single whorl or into several whorls, with a specific position relative to the petals. The gynoecium consists of carpels bearing ovules (megasporangia). Carpels can be free, or more often fused into an entity enclosing the ovules or seeds. Besides carpels and stamens, some flowers have sterile structures (staminodes or carpellodes) or other emergences of the receptacle. These are often developed as nectaries and can be conspicuous.

Another characteristic besides leaves that flowers share with the vegetative parts of the plants is the phyllotaxis or order of initiation of floral organs (see p. 28). The transition in phyllotaxis from the vegetative shoot to the flower can be gradual or abrupt and is mediated by bracts and sepals. The calyx usually continues the same spiral sequence as vegetative leaves. There is generally a disruption in the initiation sequence between sepals and petals, leading to an alternation of whorls. The result of the phyllotactic sequence is a relatively stable position of floral parts relative to each other, which is fundamentally important in understanding and interpreting the structure of the flower.

Complex versus reduced flowers

The development of flowers is correlated with mode of pollination. There is a marked difference between flowers with a biotic (animal) pollination syndrome and those with an abiotic syndrome (wind or water). Animal pollination is accompanied by a series of adaptations to attract specific pollinators and to protect the floral parts from damage. Differentiation of protective sepals and carpels, nectaries, showy petals and stamens is part of the arsenal leading to effective fertilization. Depending on the pollinating animal, different

strategies were developed to increase the success of pollination, occasionally leading to complex flowers or inflorescences. Wind pollination is accompanied by a syndrome of characters, such as small, unisexual flowers, loss of petals or reduction of the perianth, long styles and filaments, production of a large amount of pollen, lack of viscin in pollen, and reduction in the number of ovules (e.g. Linder, 1998; Friedman and Barrett, 2008).

Reversals in the pollination syndrome occur frequently in the angiosperms. Secondary wind-pollinated flowers occur in all major clades with a predominance of insect pollination (e.g. *Thalictrum* in Ranunculaceae, *Sanguisorba* in Rosaceae, *Macleaya* in Papaveraceae, some *Acer* in Sapindaceae, some *Erica* in Ericaceae, *Fraxinus* in Oleaceae, *Xanthium* in Asteraceae, *Theligonum* in Rubiaceae, *Leucadendron* in Proteaceae). Larger, predominantly wind-pollinated clades include Fagales and Poales. Wind-pollinated clades sometimes include species that have reverted to insect pollination (e.g. *Trochodendron* in Trochodendraceae, *Castanea* in Fagaceae, Buxaceae).

Specific elaborations of petals and/or staminodes are clearly linked with pollination syndromes and are triggered by the kind of pollinators that evolved with the flowers. Secondary stamen and carpel increases are widespread in the core eudicots, and are linked with the potential for higher pollen or ovule supply. Very often, there is a close mechanical correlation between petals and stamens, or stamens and style, in the release of pollen or the protection of the anthers. Different elaborations on the petals are also directly linked to the pollinator (e.g. the building of landing platforms, nectar containers and nectar guides: see Endress and Matthews, 2006b).

Flowers are morphologically highly dynamic entities with a potential for evolution reaching far beyond our preconceived ideas of the limitations of floral evolution. This flexibility is closely linked with what is available at the organ level.

1.2 Floral organs

1.2.1 Perianth

> If treated in isolation, there is no character combination which could stringently prove an organ's nature as a petal or sepal. (Endress, 1994: 26)

The perianth is the envelope of sterile leaves enclosing the fertile organs of the flower. The perianth is either differentiated into sepals and petals, or undifferentiated (perigone or tepals). In the latter case the perianth can be green (sepaloid) or pigmented (petaloid). A distinction between sepals and petals is applicable only when two different series of perianth parts are found. In cases

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with more than two whorls the transition between sepals and petals can be progressive with blurred limits.

In some cases there is unclear distinction between the perianth and surrounding bracts. In others, bracts can be variably associated with the flower, often in the form of an epicalyx, or sometimes as a fused cap (calyptra). Bracts can be distinguished from the perianth by presence of axillary buds (never in floral organs) and differences of plastochron (see p. 28; transition of a decussate to spiral phyllotaxis: Buzgo, Soltis and Soltis, 2004). Endress (2003a) suggested that bracts should be considered as phyllomes with a lower complexity than tepals. However, I believe that a distinction between bracts and tepals is sometimes impossible to make, given the existence of intermediate organs and the easy incorporation of bracts in the flower. Inclusion of bracts at the base of the flower makes the perianth bipartite, as in Magnoliaceae. Some taxa have transitional stages between bracts and tepals (in German called *Höchblätter*), as in Myrothamnaceae and some Ranunculaceae.

The distinction between sepals and petals is not always clear. If only a single whorl of perianth parts is present, it is sometimes difficult to categorize members of this whorl as sepals or petals, because one whorl may have been lost. A distinction is sometimes made between primary apetaly (as in basal angiosperms with tepals and no distinction between perianth parts) and secondary apetaly (apopetaly: Weberling, 1989), in cases where evidence exists that petals have been present and have been lost during evolution. Sepals are petaloid in several families or can have a mixed nature (partly green and pigmented; e.g. *Impatiens, Polygala*). One of the reasons for this variability is that the perianth can change function at different stages of the development of the flower. In general, the calyx tends to protect inner organs and is photosynthesizing. Later, it can become attractive for the dispersal of fruits (e.g. in *Physalis*). The main purpose of petals is to attract pollinators but they can become transformed into protective organs or dispersal units (e.g. in *Coriaria*).

The origin of the perianth has been discussed in several textbooks and papers, with various interpretations for the origin of petals: either from stamens, from bracts, from both structures, or as something totally new (see Ronse De Craene, 2007, 2008 for a recent review). In general, recent evidence from morphological and evo-devo studies suggests that petals in the majority of angiosperms are derived from bract-like structures and are homologous to the sepals in the flower. Contrary to a general assumption, cases where petals are unequivocally derived from stamens are rare in the angiosperms. In other groups, petals have variously evolved by insertion of bracts in the confines of the flower and their differentiation into two functional whorls.

An undifferentiated perianth was reconstructed as ancestral for the angiosperms in recent phylogenetic studies (Soltis *et al.*, 2005). In basal angiosperms, attraction and protection are combined with pigmentation of the entire perianth. A differentiated perianth has evolved independently several times, at least once at the base of core eudicots (Ronse De Craene, 2008).

Undifferentiated perianth (tepals or perigone)

An undifferentiated perianth tends to be concentrated in the basal angiosperms and monocots, and is usually associated with spiral or trimerous flowers. A distinction needs to be made between a primary undifferentiated and a secondary undifferentiated perianth. In the first case, tepals have evolved from bracts that became associated with reproductive organs and have acquired secondary functions of protection and attraction of pollinators. This kind of perianth is usually spiral, with a gradual differentiation from outer bract-like to inner petaloid tepals (e.g. Austrobaileyaceae, Calycanthaceae). Alternatively, two trimerous perianth whorls of several monocots are undifferentiated and petaloid. However, the switch between sepals and petals can be easy in these cases (Ronse De Craene, 2007). A secondarily undifferentiated perianth arises by loss of either the calyx (e.g. Santalaceae) or the corolla (e.g. Cunoniaceae) and should be referred to as a reduction.

Calyx

Sepals have a spiral initiation sequence with rapid growth, a broad base, three vascular traces and an acuminate (pointed) tip. The homology of sepals with leaves is based on similar anatomy as well as on several characteristics such as the presence of stipules and stomata, and sepals are often compared to the petiole of a leaf due to their broad shape (Guédès, 1979). On the contrary, petals often arise nearly simultaneously and have a delayed growth. They have a narrow base with only a single vascular trace and the tip is bifid or emarginated. Characteristics are more closely comparable to stamens than to leaves (Ronse De Craene, 2007).

Sepals can be fused together (gamosepaly). This fusion is often congenital at their margins, leaving free calyx teeth. Sepals are more often persistent than deciduous; very often, they increase in size after pollination and function in fruit dispersal. Reduction of sepals or their transformation into small scales or bristles is occasionally found in some families (e.g. in Asteraceae, Caprifoliaceae). The calyx may also vanish completely (e.g. in Santalaceae), leaving a single petal whorl combining attraction with protection of the flower.

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Corolla

The corolla, or petals, represents the inner perianth whorl of the flower and is usually pigmented (petaloid). The number of petal whorls can be high, as in Annonaceae or Berberidaceae (up to four whorls). Petals can sometimes be highly distinctive, with a claw (a narrow base, compared with a broadened base in sepals), or they can be indistinct from sepals.

The corolla can be highly elaborate by development of ventral appendages, fimbriate margins or extended tips. Petals are often trilobed, with a protruding middle lobe (e.g. Saxifragaceae) or extensive lateral lobes (e.g. Elaeocarpaceae). Bilobed petals can be formed by reduction of the central lobe (Endress and Matthews, 2006b).

In some families, petals are highly elaborate in relation to specific pollination mechanisms. For example, Byttnerioideae (Malvaceae) have petals as inverted spoons, with a hood-like base and an extended apex. More examples were given by Endress and Matthews (2006b), who suggested that there is a correlation between the smaller size or reduction of petals and elaborations on the petal surface. However, petal reduction or loss is linked with other factors, such as petaloidy of sepals and the development of a hypanthium (Ronse De Craene, 2008). Fusion of petals (sympetaly) is a frequent phenomenon in angiosperms that occurs independently or is closely linked with the evolution of the androecium. Petal tubes appear to regulate access to flowers by a variable extent of development.

1.2.2   Androecium

The androecium consists of stamens, which make up the male part of the flower. Stamens are relatively uniform. They mostly consist of four pollen sacs arranged in two lateral thecae grouped in an anther that is linked by a connective to a filament. The orientation of anthers can be inward (introrse), lateral (latrorse) or outward (extrorse). Stamens can be basally connected into a tube (e.g. Meliaceae, Malvaceae) or fused with the petals in a common tube (e.g. Caricaceae, Rubiaceae). Anthers may become laterally connivent or fuse postgenitally (e.g. Asteraceae). The number and position of stamens appear to be the most variable in the flower compared with other floral organs, but this variation is never randomized and relatively conservative in angiosperms. Flowers with more than two stamen whorls are rare and largely restricted to basal angiosperms and some basal monocots. In other instances they are the result of a secondary increase (see p. 10: e.g. Molluginaceae, Rosaceae).

When there is only a single whorl, stamens are either inserted opposite the sepals (haplostemony: e.g. Gentianaceae, Violaceae), or less frequently
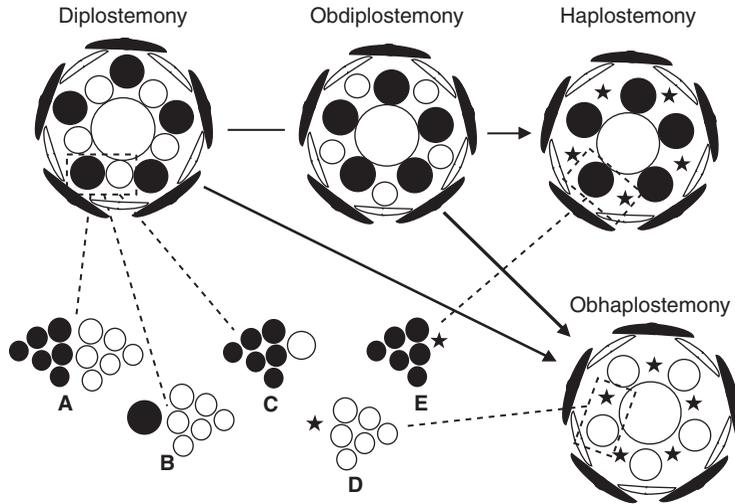
Fig. 1.1. Diagram representing possible changes in the androecium of a pentamerous flower with two stamen whorls. Black dots, antesepalous stamens; white dots antepetalous stamens; asterisk, lost stamen position or staminode. A, increase of antesepalous and antepetalous stamens; B, increase of antepetalous stamens only; C, increase of antesepalous stamens only; D, sterilization or loss of antesepalous stamens and increase of antepetalous stamens; E, sterilization or loss of antepetalous stamens and increase of antesepalous stamens.

opposite the petals (obhaplostemony: e.g. Vitaceae, Primulaceae). When two stamen whorls are present, they arise separately and are often spatially separated (Fig. 1.1). The number of stamens is ten in pentamerous flowers or eight in tetramerous flowers, a common pattern among rosids. Diplostemony is the condition where the outer stamen whorl is situated opposite the sepals and the inner whorl opposite the petals (e.g. Coriariaceae, Burseraceae). Obdiplostemony is the opposite condition, with outer stamens opposite the petals (e.g. Geraniaceae, Saxifragaceae). The distinction between diplostemony and obdiplostemony is often the result of developmental constraints. Obdiplostemony is caused by the pressure of developing carpels resulting in more outward orientation and shift of the antepetalous stamens (e.g. Ericaceae, Rutaceae: Leins, 1964a; Eckert, 1966; Ronse De Craene and Smets, 1995b). In some groups of plants, the antepetalous stamens arise before the antesepalous stamens; this inverted development is often linked with weakening or sterilization of the antesepalous stamens (e.g. Malvaceae). Obdiplostemony is often a first step towards evolution of (ob)haplostemony. This pattern may be related to a conversion of one whorl into staminodes.

Staminodes

Staminodial structures are defined as sterile stamens. The main criterion in recognizing staminodial structures is that of position, as any emergences in the flower can arbitrarily be called staminodial (Leins and Erbar, 2007). Rarely, the presence of sterile anthers is an indication of a former function as stamens. Staminodes are widely scattered in the angiosperms (e.g. Walker-Larsen and Harder, 2000; Ronse De Craene and Smets, 2001a), and are the result of sterilization affecting a complete whorl of stamens, or a variable number of stamens within a whorl. Sterilization of stamens has evolved frequently in angiosperms; for example, it affects 72% of all families of rosids (Walker-Larsen and Harder, 2000). In cases where an entire stamen whorl becomes obsolete, stamen remnants may still be identified in flowers, but they will eventually disappear and this process is irreversible. However, in many instances loss of fertility was accompanied by acquisition of novel functions not performed by stamens, such as differentiation into food-bodies (*Calycanthus*), osmophores (*Austrobaileya*), building of nectar containers (e.g. Loasaceae), enhanced optical attraction (Theophrastaceae, Eupomatiaceae), differentiation into nectaries (e.g. *Helleborus* in Ranunculaceae) or a combination of these (*Ranunculus*, *Aquilegia*). This process offers new evolutionary potential in many groups of plants. Walker-Larsen and Harder (2000) argued that sterilization of stamens within a whorl is evolutionarily reversible, such as in Lamiales, where the adaxial staminode can be restored to a fully fertile stamen by a reversal to polysymmetry. However, there is a threshold beyond which such a reversal is impossible.

The presence of staminodes is important in floral diagrams as it indicates evolutionary transitions in stamen numbers or changes in flower configurations.

Polyandry

In cases where the number of stamens is higher than double the number of petals or sepals the androecium is polyandrous. However, various non-homologous forms of polyandry exist in the angiosperms. Polyandry can be primary, by initiation of a high number of stamens in whorls or following the spiral initiation of a flower, or secondary (complex) by division of primary (common) primordia into secondary stamens (Fig. 1.1; Ronse De Craene and Smets, 1987, 1992a). In the past a fundamental distinction was made between many and few stamens, the former being interpreted as ancestral. However, the mere distinction between many and few stamens is simplistic and is not reflected in the development of polyandry.

Primary polyandry ('true polyandry') implies that a high number of stamen primordia arise in a specific sequence in the flower, whereas each primordium

develops into a single stamen. Primary polyandry can be spiral or whorled, depending on the merism of the flower (see p. 30). Trimerous or dimerous flowers with multistaminate androecia in several whorls often show an alternation of paired and unpaired stamens (e.g. Papaveraceae). With primary polyandry, initiation of stamens is usually centripetal, though it can be reversed to a centrifugal development (e.g. Alismatales) due to spatial constraints.

In the case of secondary polyandry, the number of stamens is increased by developmental multiplication of stamen primordia. This development is fundamentally different from spiral or whorled polyandry, which is characterized by genesis of one stamen per primordium. A stamen primordium can divide into a pair or higher number of stamens, which may initiate in different directions (centrifugally, laterally or centripetally), depending on spatial constraints (Ronse De Craene and Smets, 1987, 1992a). The development of complex polyandry proceeds from one or two whorls of stamens (Fig.1.1). In some cases, the boundaries of the initial stamen primordium (primary or complex primordium) can be identified and the secondary stamens appear fused into groups or fascicles. The stamens remain united at the base and they have a common vascular supply (trunk bundles). Secondary polyandry can be linked with diplostemony, when one whorl remains simple while the other is multiplied (e.g. *Reaumuria* in Tamaricaceae: Ronse De Craene, 1990), or when the other whorl becomes staminodial (e.g. several Malvaceae). Very often, only a single initial whorl is present in the flower (e.g. *Hypericum*). Polyandry becomes much more complicated when the identity of separate primordia is lost by development of a ring primordium (ring wall). Stamen groups may still be discernible on the ring (e.g. Malvaceae), or a high number of stamens arise in girdles without clear boundaries between stamen groups. The advantage of a ring primordium is that a very high number of small stamens can develop, considerably increasing the pollen load. The direction of stamen development is often centrifugal and can be ongoing when the carpels are initiated. The growth of the receptacle or hypanthium can influence the extent of the secondary increase of stamens and the direction of development (see p. 20; Ronse De Craene and Smets, 1991a, 1992a).

The general pattern of the androecium in the angiosperms probably evolved from a moderate number of stamens arranged in a spiral (e.g. *Amborella*). Different evolutionary lines led to an increase or reduction in stamen number, with several transitional steps. An outline of this evolutionary progression is shown in Fig. 1.2 (Ronse De Craene and Smets, 1998a). As stamen number decreases and positions become fixed, it is possible to characterize specific 'types' of androecia. From primary polyandrous flowers, further increases or reductions can evolve, leading to much higher or lower numbers of stamens. In the case of whorled polyandry (polycycly), the number of whorls